

Sexual expression and mating system in watermelon: implications for breeding programs

Maria Aldete Justiniano da Fonseca Ferreira^{*1}; Manoel Abílio de Queiróz²; Roland Vencovsky³; Leila Trevisan Braz⁴; Maria Lúcia Carneiro Vieira³ and Rita Mércia Estigarribia Borges⁵

¹Embrapa Roraima, Caixa Postal 133, CEP 69301-970, Boa Vista, RR, Brazil; ²Embrapa Semi-Árido, Caixa Postal 23, CEP 56300-970, Petrolina, PE, Brazil; ³Depto. Genética da ESALQ-USP, Caixa Postal 83, CEP 13400-970 Piracicaba, SP, Brazil; ⁴Depto. Horticultura-FCAV-UNESP, Rod. Paulo Donato Castellane km 5, CEP 14870-000 Jaboticabal, SP, Brazil; ⁵Escola Agrotécnica Dom Avelar Brandão Vilela, Caixa Postal 178, CEP 56300-000, Petrolina, PE, Brazil. (*Corresponding Author. Email: aldete@cpafrr.embrapa.br)

ABSTRACT

This study had the following objectives: to investigate the sexual expression in seven watermelon populations; to evaluate some population parameters and the genetic potential of a population (PCS) obtained by crossing and segregating for sexual expression and other traits. For verifying the sexual expression, populations were evaluated with respect to type of flower, under controlled conditions. Maternal and selfed progenies were obtained from the PCS population for field evaluation, considering: fruit yield per plant, fruit weight, number of fruits per plant, flesh colour and sugar content. On the basis of molecular marker data (RAPD), the outcrossing rate (t_m and t_s), allelic frequencies (p_i) and the coefficient of inbreeding (F) were estimated for the PCS population. Results indicated that populations B9 and P14 are andromonoecious in which natural selfing occurs, giving rise to normal fruits. The remaining populations are monoecious. Population PCS practices a mixed mating system ($t_m = 0.765$) and, having shown sufficient genetic variation and relatively low inbreeding depression, has high potential for breeding purposes. The importance of obtaining accurate estimates of the outcrossing rate is pointed out, specially because sexual expression and the mating system are genetically conditioned in watermelon populations.

KEY WORDS: *Citrullus lanatus*, mixed mating system, prebreeding, RAPD.

INTRODUCTION

Considering sexual reproduction, populations are classified according to their mating system in autogamous, allogamous, and mixed mating system or intermediate. In autogamic populations, reproduction usually happens by natural selfing. However, there may be up to five percent of natural outcrossing. On the other hand, alogamic populations reproduce through natural outcrossing and eventually by natural selfing up to five per cent. Mixed or intermediate populations present outcrossing rates from 5% to 95%.

Adequate breeding programs depend on the knowledge of the mating system of a population since methods are applied according to the specific and prevailing reproduction system of that population. Distinct genetic population structures occur under outcrossing and/or selfing, in natural conditions. In addition, inbreeding that takes place naturally when the aim is to evaluate components of genetic variance. Under outcrossing it is assumed that individuals

within an open pollinated family are half-sibs. However, when some inbreeding takes place due to selfing, assuming panmixia will lead to biased estimates of the genetic parameters of a population. Also, inbreeding can increase the probability that different individuals have similar alleles, resulting in a reduction in genetic variability within families and an increase in variability among families.

On the other hand, the ways plants reproduce are influenced by many factors and one of them is sexual expression. According to Robinson *et al.* (1976), there are records of different kinds of sexual expression in cucurbits. In spite of being genetically controlled, this expression is also affected by other factors such as temperature, humidity, fertilization and growth regulators. Studies on watermelon, for instance, have shown monoecious and andromonoecious populations. In the former, there are male and female flowers and in the latter there are male and hermaphroditic ones. These traits are controlled genetically by a single pair of genes, being andromonoecism (*aa*) recessive in relation to monoecism (*A_*) (Rhodes and Zhang, 1995).

Among cucurbits of commercial importance, the cucumber is the one that shows greater variability for sexual expression. Their populations can be andromonoecious, androecious (plants with only male flowers), gynoecious (plants with only female flowers), hermaphrodites, monoecious and trimonoecious (plants with male, female and hermaphroditic flowers). In the case of the melon, most of the American populations are andromonoecious, while the Asian and Indian ones are monoecious. There are also other populations that are androecious, gynoecious, gynomonoecious (plants with more female than hermaphroditic flowers), hermaphrodites and trimonoecious. A smaller variability is found in watermelon and pumpkin, and most pumpkin cultivars are monoecious (Robinson *et al.*, 1976). For the ridged luffa or vegetable sponge (*Luffa acutangula*), the different forms of sexual expression are similar to those of the cucumber, while the bottle gourd (*Lagenaria siceraria*) is strictly monoecious, except for one andromonoecious variant found in a segregating population (Singh *et al.*, 1996).

There are other genes that affect the structure and fertility of flowers in cucurbits, like those controlling the male sterility in pumpkins, watermelon, melon and cucumber and the parthenocarpy in cucumber (Hexun *et al.*, 1998; Malepszy and Niemirowicz-Szczytt, 1991; Robison *et al.*, 1976; Zhang *et al.*, 1996).

Cucurbits are considered allogamous despite their large variability in sexual expression and the great environmental influence over this trait. However, Robinson *et al.* (1976) have reported that different types of sexual expression have influence on the natural outcrossing rate, since both natural outcrossing and selfing for the cucumber and melon can occur. Kohn and Biardi (1995) estimated a selfing rate of 73% in monoecious plants and 11.9% to 40.7% in gynoecious plants from two populations of *Cucurbita foetidissima*, a perennial cucurbitaceae that is native of the United States and Northeast Mexico. These estimates indicate a mixed mating system, which is intermediate in relation to autogamy and allogamy.

Allard (1960) reports that cucurbits are closer to autogamy than to allogamy, since populations may derive from a few individuals during the domestication process, due to the botanical characteristics of the plants (they are creepers with many vines and the fruits have many seeds). This may have helped outcrossings among relatives and thus reducing the genetic load along generations.

Mohr (1986) showed that in watermelon andromonoecious populations pollination takes place

with efficiency because insects visit the hermaphroditic flowers. As a consequence, there would be no advantage of andromonoecious populations over monoecious ones regarding the maintenance of pure inbred lines. Therefore, the author considers the watermelon as an allogamous species.

However, since both selfing of hermaphroditic flowers and outcrossing, with pollen coming from another plant, may occur, it is believed that andromonoecious populations may show a mixed mating system, and that depending on the selfing rate, they could be closer to autogamy. Natural selfing is less probable but obviously possible to take place in monoecious populations through the fertilization of female flowers by pollen of male flowers from the same plant. These populations may have a mixed mating system, even though closer to allogamy. For segregating populations for sexual expression, the mating system should vary from predominantly allogamous to predominantly autogamous, due to the variable frequency of monoecious and andromonoecious plants.

Andromonoecious populations in watermelon have probably evolved from monoecious ones, once the recessive allele that determines an andromonoecious individual (*a*) is kept in individuals within monoecious heterozygotes (*Aa*). While investigating the evolution dynamics of the watermelon in Northeast Brazil, a secondary centre of genetic diversity of this species, Romão (1995) found natural seed banks in the soil, as a consequence of the action of a number of factors namely, genetical (genes that determine the dormancy of the seeds and explosive rind), ecological (spreading of seeds by the guará wolf) and cultural (when people eat fruits and leave seeds on the ground). The existence of these seed banks, along with the persistence of populations under adverse conditions, and the use of different farming systems in the region, have all contributed to the development of subspontaneous populations formed by a few individuals. It is believed that mating among relatives must have occurred. This led to the fixation of alleles along generations, which were responsible for andromonoecious individuals (Vencovsky *et al.*, 2001).

Considering available informations, even under field conditions and with the presence of pollinator insects, it is believed that natural selfing in andromonoecious and monoecious populations is perfectly possible. Depending on the natural selfing rate these populations may have a mixed mating system.

Therefore, the main goals of this work were: a) to evaluate the sexual expression of some watermelon populations, to verify whether or not natural selfing

takes place; b) to estimate the natural outcrossing rate in segregating populations for sexual expression; c) to discuss the implications of the sexual expression to breeding programs and d) to estimate quantitative parameters.

MATERIAL AND METHODS

In this study, materials and methods are described as follows:

Sexual Expression

The traditional populations B9, B13, P14 and M7, collected in the Northeast of Brazil (Bahia, Pernambuco and Maranhão, respectively) (Queiróz 1993, 1998), as well as the American varieties Crimson Sweet, Charleston Gray and New Hampshire Midget, were evaluated in a greenhouse protected from pollinator insects. The greenhouse is located in the Horticultural and Medicinal Plants Department at the School of Agrarian and Veterinary Sciences (UNESP) in Jaboticabal – SP, from January to April 1995. The experiment was set in four randomized blocks, with four replications and eight plants per plot. At flowering time, besides observing the emergence of male flowers, 100 observations were made, at random, per population, counting the number of female and hermaphroditic flowers. The occurrence or not of natural selfing in the hermaphroditic flowers, as well as the formation of fruits, were also observed.

Segregating population PCS

During 1996 and 1998, a base population was synthesized in order to combine the characteristics of population P14 (high yield, small fruits and resistance to powdery mildew) with the commercial variety Crimson Sweet (high soluble solid contents and flesh of intense red colour). In addition, populations P14 and Crimson Sweet are clearly andromonoecious and monoecious, as it could be observed in a previous greenhouse experiment.

Initially, 100 hand pollinations were carried out taking 100 individuals from each population, producing up to 100 F_1 fruits. Subsequently, a population of 1000 individuals was established through a mixture of 10 seeds from each F_1 fruit, which reproduced naturally in an isolated field. A single fruit was chosen, at random, from each plant of this population, and two seeds were taken from each fruit, randomly as well. This bulk of

2000 seeds formed the base population PCS.

Population PCS was installed in an isolated field and at flowering time plants were evaluated for their sexual expression. Sixty-four plants for seed parents were also sampled at random, each one giving rise to an open pollinated or maternal progeny (PL) and one selfed or S_1 (AF) progeny. The term family is used to indicate the group of offspring (PL and AF) of a given seed parent and the term progeny to indicate siblings of a given type (PL or AF). From the 64 progenies, 12 were sampled at random for molecular analysis to determine the natural outcrossing rate. Thus, molecular data were obtained through RAPD genotyping and the corresponding maternal progenies, with 23 individuals each. Primers BO2, B14, CO4 and C16 gave origin to 16 polymorphic loci; however, only nine were used in this study.

The natural outcrossing rate was estimated by maximum likelihood, considering the mixed mating system model established by the software MLDT (Multilocus Estimation of Outcrossing with Dominant Markers). The outcrossing rate was estimated by all loci simultaneously (t_m multilocus) and each individual loci (t_s single locus), which corresponds to the average of the estimate of each locus individually (Ritland, 1990). The allelic frequency (p_i) and Wright's (F) inbreeding coefficient of the population were also estimated.

Maternal and selfed families were evaluated at the Experimental Station of Bebedouro, Petrolina-PE (EMBRAPA Semi-Árido Research Center), in two experiments, with three replications.

To evaluate the genetic potential of population PCS, the following traits were considered: fruit yield per plant (PP) (kg/plant); average fruit weight (PF) (kg); number of fruits per plant (NF); flesh colour (CP) (score 1 was given to intense red, 2 for the red colour, 3 for the light red, 4 for the pink colour and 5 for the white colour) and total soluble solid contents (TS) (°Brix).

As mentioned earlier, this population was derived from the crossing of contrasting parents in relation to sexual expression and other characteristics of commercial importance.

RESULTS AND DISCUSSION

Sexual Expression

Results showed that all assessed populations bore male flowers first and then the female and

hermaphroditic ones. The percentages presented here refer to female and hermaphroditic flowers only. Populations B9 and P14 bore 100% of hermaphroditic flowers, thus indicating that they are andromonoecious. Crimson Sweet and New Hampshire Midget bore 92% to 97% of female flowers, respectively, indicating that these populations are mainly monoecious. On the other hand, populations Charleston Gray, B13 and M7, with 100% of female flowers, are typically monoecious (Figure 1). Moreover, the occurrence of natural selfing, with the development of normal fruits, was verified in all the hermaphroditic flowers found in populations B9 and P14, which is an evidence of pollen viability.

Segregating population PCS

Outcrossing Rate

Plants from the segregating population PCS bore 53.5% of female flowers, thus being monoecious, and 46.5% of andromonoecious flowers. Table 1 shows the estimates of the frequency of dominant alleles, the outcrossing rates t_m and t_s , as well as the inbreeding coefficient. Three groups of estimations were obtained. The first considered all progenies jointly and the others took only progenies stemming from andromonoecious or monoecious seed parents.

The outcrossing rate for all progenies varied from 73.2% to 76.5%, showing that population PCS has a mixed mating system. This rate tended to be larger in monoecious progenies than in andromonoecious ones. These results were expected, since under isolated greenhouse conditions natural selfing in andromonoecious plants from population P14 was verified. Inbreeding rates for these individuals were also expected to be greater than the rate for monoecious ones, and this was confirmed through the estimates of the inbreeding coefficient. It should be pointed out that the use of dominant markers is perfectly adequate for estimating the outcrossing rate. There are examples in the literature (Gaiotto *et al.*, 1997) showing good agreement between estimates of t obtained through dominant (RAPD and AFLP) and codominant markers.

Estimates of the inbreeding coefficient ($\hat{F} = 0.091$) also indicated a mixed mating system for this population but tending to allogamy. Under inbreeding equilibrium, the expected value was $\hat{F} = (1 - \hat{t}) / (1 + \hat{t}) = 0.133$, which is slightly higher than the former estimate. This result may indicate an excess of heterozygotes in the segregating

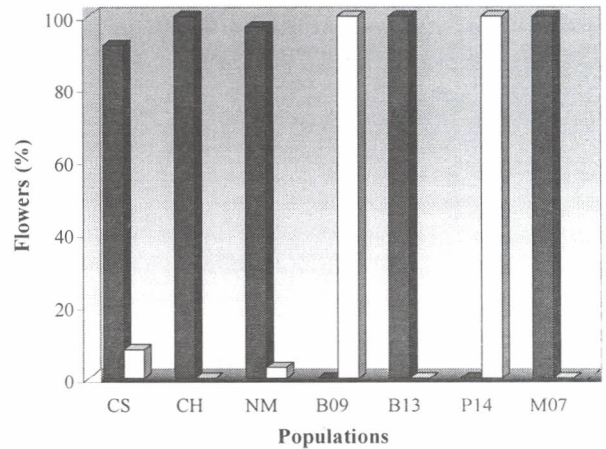


Figure 1. Percentage of female (black) and hermaphroditic (white) flowers, excluding male flowers, in seven watermelon populations. Populations: CS= Crimson Sweet; CH= Charleston Gray; NM = New Hampshire Midget and B09, B13, P14 and M7 = traditional watermelon populations from the Cucurbit Germplasm Bank.

population investigated. This is expected from an intervarietal hybrid, derived from very contrasting parents and highly heterozygotic such as population PCS. Another factor that may have contributed to this relative excess of heterozygotes is a possible selection against homozygotes, as a consequence of inbreeding depression at the seedling stage. Since seedlings were grown in trays and later transplanted, non-intentional selection may have occurred during this phase. Actually, a variation in the seeds germination percentages was verified. Some germinated later than others, conditioning more or less vigorous seedlings.

It should be pointed out that the investigated segregating population has not yet reached inbreeding equilibrium. This stage is reached asymptotically under open pollination. It is expected from the PCS homozygosity to be below the equilibrium point, as it was confirmed by $\hat{F} = 0.091 < 0.133$. However, it is worth investigating which proportion of homozygotes (x) should have been reached, as discussed by Pereira *et al.* (1986) in Ferreira (2000). Considering the most extreme diverse situation among parental varieties (P14 = A_1A_1 and CS = A_2A_2 for a given locus A), the F_2 plants studied here should be in the proportion of $1/4$, $2/4$, $1/4$ for genotypes A_1A_1 , A_1A_2 and A_2A_2 , respectively. This is valid for any value of s . According to the Wright's model, these genotypic frequencies are $p^2 + pqF$, $2pq(1 - F)$ and $q^2 + pqF$ for genotypes A_1A_1 , A_1A_2 and A_2A_2 , respectively. At an equilibrium point, the frequencies

Table 1. Estimates of the allelic frequencies of dominant markers (p_i), goodness-of-fit (χ^2) to the mixed mating system model, outcrossing rates based on all loci simultaneously (t_m), and on a single locus bases (t_s) and inbreeding coefficient (F).

| RAPD loci | Allelic frequencies (p_i) | χ^2 | $P^{1/}$ |
|--------------------------|-------------------------------|---------------|----------|
| C16-1050 | 0.700 (0.052) | 0.32 | 0.5716 |
| C16-500 | 0.779 (0.038) | 0.95 | 0.3297 |
| B14-2600 | 0.507 (0.064) | 2.17 | 0.1407 |
| B14-2200 | 0.060 (0.014) | 0.15 | 0.6985 |
| B14-1400 | 0.508 (0.097) | 0.53 | 0.4666 |
| B14-1000 | 0.841 (0.038) | 0.20 | 0.6547 |
| B14-900 | 0.383 (0.076) | 1.98 | 0.1594 |
| B14-700 | 0.524 (0.046) | 2.15 | 0.1426 |
| C04-950 | 0.634 (0.068) | 0.01 | 0.9203 |
| All families | | | |
| | t_m | 0.765 (0.056) | |
| | t_s | 0.732 (0.059) | |
| | F | 0.091 (0.079) | |
| Andromonoecious families | | | |
| | t_m | 0.646 (0.248) | |
| | t_s | 0.655 (0.181) | |
| | F | 0.414 (0.206) | |
| Monoecious families | | | |
| | t_m | 0.815 (0.099) | |
| | t_s | 0.806 (0.106) | |
| | F | 0.075 (0.250) | |

^{1/} $P = \chi^2$ levels of probability.

0.2832; 0.4335 and 0.2832 are expected for these genotypes, accepting that $p = q = 0.5$, and considering $\hat{s} = 1 - \hat{t}_m = 0.235$ as a valid estimate for future generations. However, for the investigated population, these genotype frequencies should be 0.2728; 0.4545 and 0.2728 by considering $\hat{F} = 0.091$. The proportion x suggested by Pereira *et al.* (1986) in Ferreira (2000), is expressed by $x = (H_1 - H_N)/(H_1 - H_\infty)$, where H is of homozygosity measures. In the case of this population, $H_1 = 0.50$, $H_N = 0.2728 + 0.2728 = 0.5456$ and $H_\infty = 0.2832 + 0.2832 = 0.5664$. Hence $x = 0.687$, meaning that it took only one generation of open pollination to generate the segregating population. 68.7% of the total homozygosity increment to reach equilibrium had already been achieved.

Further investigations should look into the additional number of generations (N) needed for population PCS to reach at least 90% of the expected homozygosity for inbreeding equilibrium. Since $\hat{s} = 0.235$ and $N = \log [(1 - x)\hat{s}/2] / \log (\hat{s}/2)$ (Pereira *et al.*, 1986 in Ferreira 2000), it is concluded that one additional generation would be sufficient for this population to reach the expected 90% of homozygous equilibrium condition. With this additional generation this study

would be more suitable for quantitative genetics studies. In addition, it would generate more transgressive and commercially desirable individuals, since one more generation of recombination would take place. Assuming that the progenies of open pollination taken from this segregating population have already reached 90% of homozygosity at equilibrium and that they were produced after two generations of open pollination, it would be adequate to take a bulk of seeds from these progenies and generate a new base population for extraction of new progenies.

In conclusion, it was verified that the watermelon PCS population has a mixed mating system, and that its outcrossing rate had a tendency to alternate from monoecious to andromonoecious progenies. It was also noted an excess of heterozygotes in relation to what is expected from an inbreeding equilibrium. Even though it did not reach the ideal equilibrium condition, it showed a satisfactory 68.7% rate for a possible homozygous condition. This population is genetically closer to allogamy than to autogamy despite having a mixed mating system.

Handling of a population with a mixed mating system is closer to allogamy, especially in relation to quantitative genetics. However, such a situation offers some advantages, as it will be discussed later in this paper.

Genetic variance

The evaluation of the maternal and selfed progenies showed that this population contains genetic variance for all analyzed traits (significant P effects). PCS is therefore a very promising population to be exploited in plant breeding programs. The difference between PL and AF overall means was significant for the traits PF, CP and TS. This was detected through the significance of types of progeny effects (T effect) as well as the family x types interaction. Results showed inbreeding depression, which varied among progenies (significance of the P x T interactions; Table 2).

Expressive progeny effects were detected for all traits in both PL and AF progenies. This clearly demonstrates that there are genetic differences among progenies within each type, and indicates the potential genetic variability of this population. This is especially true for traits related with fruit yield where a large range of variation was observed for both PL and AF progeny means. Variables PP, PF and NF showed a range of 24.5 kg/plant; 3.4 kg/fruit and 15.3 fruits/plant for PL progenies and of 30.8

kg/plant; 4.6 kg/fruit and 12.4 fruit/plant for the AF progenies, respectively. However, the experiment coefficients of variation were high for these traits, implying low experimental precision. High values of the coefficient of variation for these traits are to a certain extent expected, once they tend to be more influenced by the environment than other characteristics (Table 2). On the other hand, to evaluate more precisely the real effect of inbreeding depression on watermelon, additional studies are needed which would take into account different levels of inbreeding as well as better environmental control.

Final Considerations

For populations with mixed mating system, the coancestry among individuals of the maternal families is higher than expected under allogamy. This implies that the estimates may be wrong if the F rate is considered zero. The genetic variance (σ^2_G) of such

populations involves other components besides additive (σ^2_A) and the dominance (σ^2_D) variances, and is: $\sigma^2_G = (1+F)\sigma^2_A + (1-F)\sigma^2_D + 4FD_1 + FD_2 + F(1-F)H^* + (F_c - F^2)(H^2 - H^*)$. The component D_1 is a covariance between the additive effects and dominance effects of the homozygotes; D_2 is the variance of dominance effects of the homozygotes, H^* and H^2 are components of inbreeding depression and F_c is the joint inbreeding coefficient for two loci. Among these components, D_1 deserves the greatest attention, as it represents a covariance and it may be negative. In this case, it contributes to the reduction of the genetic progress (Cockerham and Weir, 1984).

As more than one generation of random pollination is required to reach equilibrium, these populations show three types of genetic progress: (1) immediate progress (P_{GI}), which is the progress in the generation immediately after selection; (2) permanent progress (P_{GP}), which is the progress reached when the selected population returns to

Table 2. Synthesis of the analysis of variance for fruit yield per plant (PP) in kg/ha; average fruit weight (PF) in kg; number of fruits per plant (NF); flesh color (CP) and sugar content (TS), with overall means and the range observed for all traits.

| Sources of variation | DF | Mean Squares | | | | |
|---------------------------------------|-----|-----------------------|----------------------|-----------------------|----------------------|----------------------|
| | | PP | PF | NF | CP | TS |
| Trials | 1 | 1163.8108 | 9.0279 | 3.9144 | 16.5399 | 0.0709 |
| Replications/Trials | 4 | 213.9665 | 1.6229 | 91.1616 | 0.1559 | 2.5850 |
| Families (P)/Trials | 62 | 68.7637 ^{1/} | 4.3247 ^{1/} | 33.0839 ^{1/} | 2.6574 ^{1/} | 3.9910 ^{1/} |
| Error a/Trial | 124 | 62.5580 | 0.5381 | 10.4325 | 0.2109 | 0.3137 |
| Types of progenies (T)/Trials | 2 | 46.0351 ^{ns} | 5.2116 ^{1/} | 58.0410 ^{ns} | 2.4236 ^{1/} | 3.9652 ^{1/} |
| Error b/Trials | 4 | 25.1535 | 0.2218 | 0.2861 | 0.0973 | 0.1520 |
| P x T interaction | 62 | 35.7665 ^{ns} | 0.8288 ^{1/} | 10.0883 ^{ns} | 0.6685 ^{1/} | 1.1106 ^{1/} |
| Error c/Trials | 124 | 30.8680 | 0.4380 | 11.6879 | 0.2134 | 0.2985 |
| Family plus P x T interaction effects | | | | | | |
| Progenies/PL | 63 | 59.7621 ^{1/} | 1.8789 ^{1/} | 23.5317 ^{1/} | 1.5097 ^{1/} | 1.8821 ^{1/} |
| Progenies/AF | 63 | 61.6817 ^{1/} | 3.3466 ^{1/} | 19.1155 ^{1/} | 2.0436 ^{1/} | 3.1688 ^{1/} |
| Error d/Trials | 248 | 46.7130 | 0.4881 | 11.0602 | 0.2122 | 0.3061 |
| Coefficients of variation | | | | | | |
| C.V. (a) % | | 47.33 | 22.16 | 43.91 | 13.71 | 7.57 |
| C.V. (b) % | | 30.01 | 14.23 | 7.27 | 9.31 | 5.27 |
| C.V. (c) % | | 33.25 | 19.99 | 46.48 | 13.79 | 7.38 |
| C.V. (d) % | | 40.90 | 21.12 | 45.22 | 13.75 | 7.48 |
| Means | | | | | | |
| Progenies PL ^{2/} | | 17.18 | 3.15 | 7.89 | 3.45 | 7.27 |
| Progenies AF ^{2/} | | 16.24 | 3.47 | 6.82 | 3.25 | 7.53 |
| Range | | | | | | |
| Progenies PL | | | | | | |
| Lower value | | 7.31 | 1.61 | 3.67 | 2.20 | 5.56 |
| Upper value | | 31.79 | 5.00 | 19.00 | 4.82 | 8.85 |
| Progenies AF | | | | | | |
| Lower value | | 7.19 | 1.57 | 2.50 | 1.58 | 5.42 |
| Upper value | | 38.00 | 6.22 | 14.95 | 5.00 | 10.07 |

^{1/} Significant at 0.01 level of probability and ^{ns} non-significant at 0.05 level of probability; ^{2/} PL = open pollinated or maternal family and AF = selfed progeny.

equilibrium, and (3) transient progress (P_{GT}), which is the genetic progress after P_{GI} generation after generation, until the population reaches its equilibrium. P_{GI} depends on all of the components of the genotypic variance, while P_{GP} depends only on σ_A^2 , D_1 and D_2^* , since the dominance and inbreeding depression components are eliminated along the generations (Wright and Cockerham, 1985).

Therefore, determining the outcrossing rate of the populations under study is essential because it allows a better knowledge of the genetic structure of these populations and makes quantitative studies possible. The use of biochemical and molecular markers are preponderant tools as they make the quantification of some genetic parameters of the populations possible, such as the outcrossing rate and the inbreeding coefficient.

The importance of the quantification of these parameters for watermelon populations is even more essential since sexual expression and, consequently, the reproductive system are conditioned by genetic and environmental factors. Strictly andromonoecious populations may present a higher natural selfing rate and, in this case, be closer to autogamy than to allogamy. On the other hand, monoecious populations may present a greater outcrossing rate and be closer to the allogamous ones. These facts should be pointed out for the PCS population, which is segregating for sexual expression.

In relation to populations with a mixed mating system two major points should be taken into consideration. The first one concerns pollen contamination while doing selective processes on accession and cultivar multiplications. The floral structure should be carefully isolated and emasculations should be done in the hermaphroditic flowers before pollen shed. The second refers to the occurrence of non-intentional selection during seedling development. Studying ways of breaking seed dormancy is one possible way to avoid this problem.

On the other hand, an advantageous feature of populations such as PCS, which tends more to allogamy, is that they may be submitted to recurrent selection. This type of selection procedure not only increases the frequency of favorable alleles but also allows for the recombination to take place, increasing the probability of selecting superior genotypes with commercial value.

Another great advantage of species with a mixed mating system is the fact that with simultaneous outcrossings and selfings, recombination and the

elimination of genetic load, occurs naturally. This also makes selection of segregating individuals with little or no inbreeding depression possible, as recorded by Ferreira (2000). For allogamic species there is natural recombination, however, high inbreeding depression is expected. With autogamic species, on the other hand, there is no depression, but recombination is only possible through artificial pollination.

Results obtained by this study have shown that a PCS population is indicated for recurrent selection programs. The method of cryptic hybrids (Paterniani and Miranda Filho, 1978) is one interesting scheme to be used with one or more populations aimed at superior inbred lines for synthesis of hybrids. In addition, the AF progenies performance indicated great potential for generating productive and prolific inbred lines with good fruit characteristics.

CONCLUSIONS

Considering sexual expression, populations B9 and P14 are andromonoecious, and Crimson Sweet, New Hampshire Midget, Charleston Gray, B13 and M7 materials are monoecious. Hermaphroditic flowers of B9 and P14 populations showed natural selfings and normal fruit development.

The segregating population PCS has a mixed mating system, closer to allogamy, but the outcrossing rate differs between andromonoecious and monoecious families. Thus this population may be improved through recurrent selection without the need for hand pollinations for recombination.

Population PCS has not yet reached complete inbreeding equilibrium, but it got close, since 68.7% of the possible homozygous increase was reached.

Even without complete equilibrium, population PCS exhibited sufficient genetic variation in all the investigated traits. It shows high potential for a breeding program, as well as for generating inbred lines with good plant and fruit characteristics.

The appropriate determination of the outcrossing rate of watermelon populations is very important for breeding programs, once sexual expression and consequently the reproductive system are controlled by genetic factors.

ACKNOWLEDGEMENTS

We thank all the employees from FCAV – UNESP and EMBRAPA Semi-Árido, as well as Mr. Carlos

Alberto de Oliveira and the other colleagues from the Cell and Molecular Biology Department at Escola Superior de Agricultura Luiz Queiroz (ESALQ/USP), for their technical support during this study. We'd like to also to thank Banco do Nordeste for its financial support and CNPq, CAPES and FACEPE for granting a scholarship for the first author.

RESUMO

Expressão sexual e sistema de cruzamento em melancia: implicações em programas de melhoramento

Este trabalho objetivou: investigar a expressão sexual em sete populações de melancia; avaliar alguns parâmetros populacionais e o potencial genético de uma população (PCS) obtida de cruzamento e segregante para expressão sexual e outros caracteres. A expressão sexual foi investigada, avaliando-se as populações, em condições controladas, quanto ao tipo de flor. Da população PCS obtiveram-se progênies maternas e autofecundadas, que foram avaliadas em campo em relação aos caracteres produção de frutos por planta, peso médio do fruto, número de frutos por planta, cor da polpa e teor de sólidos solúveis. Com base em dados moleculares foi estimada a taxa de fecundação cruzada (t_m e t_s), as frequências alélicas (p_i) e o coeficiente de endogamia (F) da população PCS. Em relação à expressão sexual os resultados indicaram que: as populações B9 e P14 são andromônicas, podendo nelas ocorrer autofecundações naturais e formação de frutos normais; as demais populações são monóicas. A população PCS pratica um sistema misto de reprodução ($t_m = 0,765$), tem suficiente variabilidade genética e relativamente pouca depressão endogâmica e, por isso, apresenta alto potencial para o melhoramento. Destaca-se a importância de obter estimativas consistentes da taxa de fecundação cruzada de populações de melancia, pois a expressão sexual e o sistema reprodutivo são condicionados por fatores genéticos.

REFERENCES

- Allard, R.W. 1960. Principles of plant breeding. John Wiley, New York.
- Cockerham, C.C. and Weir, B.S. 1984. Covariances of relatives stemming from a population undergoing mixed self and random mating. *Biometrics*. 40:157-164.
- Ferreira, M. A. J. da F. 2000. Sistema reprodutivo e potencial para o melhoramento genético de uma população de melancia *Citrullus lanatus* (Thunb.) Matsum. & Nakai. Ph.D. Diss. Universidade de São Paulo, Piracicaba, Brasil.
- Gaiotto, F.A.; Bramucci, M. and Grattapaglia, D. 1997. Estimation of outcrossing rate in breeding population of *Eucalyptus urophylla* with dominant RAPD and AFLP markers. *Theoretical and Applied Genetics*. 95:842-849.
- Hexun, H.; Xiaoyi, Z.; Zhencheng, W.; Qinghui, L. and Xi, L. 1998. Inheritance of male-sterility and dwarfism in watermelon [*Citrullus lanatus* (Thunb.) Matsum. and Nakai]. *Scientia Horticulturae*. 74:175-181.
- Kohn, J.R. and Biardi, J.E. 1995. Outcrossing rates and inferred levels of inbreeding depression in gynodioecious *Cucurbita foetidissima* (Cucurbitaceae). *Heredity*. 75:77-83.
- Malepszy, S. and Niemirowicz-Szczytt, F. 1991. Sex determination in cucumber (*Cucumis sativus*) as a model system for molecular biology. *Plant Science*. 60:39-47.
- Mohr, H.C. 1986. Watermelon breeding. p.33-66. In: Basset, M.I. (Ed.). *Breeding in vegetables crops*. Ed. Avi, Westport.
- Paterniani, E. and Miranda Filho, J. B. 1978. Melhoramento de populações. p.202-256. In: Paterniani, E. (Orgs.). *Melhoramento e produção do milho no Brasil*. Ed. ESALQ, Piracicaba.
- Queiróz, M.A. de. 1993. Potencial de germoplasma de cucurbitáceas no nordeste brasileiro. *Horticultura Brasileira*. 11:7-9.
- Queiróz, M.A. de. 1998. Cucurbitáceas no semi-árido do Nordeste brasileiro: resgate, conservação e uso. p.1-12. In: *Anais do Encontro sobre Temas de Genética e Melhoramento*, 15., Piracicaba, 1998. Departamento de Genética, Esalq, USP, Piracicaba.
- Rhodes, B. and Zhang, X. 1995. Gene list for watermelon (*Citrullus lanatus*). Report Cucurbit Genetics Cooperative. 18:68-84.
- Ritland, K. 1990. A series of FORTRAN computer programs for estimating plant mating systems. *Journal of Heredity*. 81:235-237.
- Robinson, R.W.; Munger, H.M.; Whitaker, T.W. and Bohn, G.W. 1976. Genes of cucurbitaceae. *HortScience*. 11:554-568.

- Romão, R.L. 1995. Dinâmica evolutiva e variabilidade de populações de melancia *Citrullus lanatus* (Thunb.) Matsum. & Nakai. em três regiões do nordeste brasileiro. M.S. Thesis. Universidade de São Paulo, Piracicaba, Brasil.
- Singh, S.P.; Maurya, I.B. and Singh, N.K. 1996. Occurrence of andromonoecious form in bottle gourd, *Lagenaria siceraria* exhibiting monogenic recessive inheritance. *Current Science*. 70:458-459.
- Vencovsky, R.; Pereira, M. B.; Crisóstomo, J. R.; Ferreira, M. A. J. da F. 2001. Genética e melhoramento de populações mistas. Cap.10. In: Nass, Luciano L.; Valois, Afonso C.C.; Melo, Itamar S. and Valadares-Inglis, Maria Cléria. Recursos Genéticos e Melhoramento de Plantas. Fundação MT, Rondonópolis.
- Wright, A.J. and Cockerham, C.C. 1985. Selection with partial selfing. I. Mass Selection. *Genetics*. 109:585-597.
- Zhang, X.P.; Rhodes, B.B.; Baird, W.V.; Bridges, W.C. and Skorupska, H.T. 1996. Development of genic male-sterile watermelon lines with juvenile albino seedling marker. *HortScience*. 31:426-429.

Received: June 07, 2001;

Accepted: December 18, 2001.